

# COMPARATIVE RICHNESS OF ZOÖPLANKTON IN COASTAL AND OFFSHORE AREAS OF THE ATLANTIC

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Between our eastern coast and Bermuda lie three zones of water which are of great biological interest because of their extreme contrast: the coastal water, overlying the continental shelf; the "slope" water, which is the area of mixing between the continental slope and the Gulf Stream; and the Sargasso water, of which the Gulf Stream is the western and northern edge. An opportunity to make a comparative investigation of the zoöplankton of the coastal zone and of the zones farther offshore presented itself during the cruises of the research vessel "Atlantis" between Montauk Point, Long Island, N. Y. and Bermuda, which were begun in 1937.

Since the primary object of these cruises was a study of the physical structure of the Gulf Stream and since the ship was working in other localities during the intervals between these cruises, the plankton hauls were necessarily "catch-as-catch-can." Although an extensive network of stations throughout the region which were revisited at frequent intervals would obviously have been desirable, the data available from a single line of stations repeated ten times between October, 1937 and June, 1939 are instructive and raise certain important questions, especially when compared with earlier observations in this area.

Our first objective in the present investigation of the plankton was a comparison of the richness of the coastal and offshore zones. For this purpose four standard stations were located at approximately equal intervals across the coastal water and four more stations were occupied in the slope water beyond (Fig. 1). A ninth station located well within the limits of the Sargasso Sea was established as typifying oceanic water far removed from any influence of the coast. Since the abundance of the plankton was expected to vary within each zone during the course of the season, and since these variations probably would not be the same in different zones, a knowledge of the seasonal cycles of the plankton formed a second objective and one upon which the first necessarily de-

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pended. Furthermore, changes in the general nature and richness of the plankton might occur from year to year. It was therefore proposed to examine our data for annual differences in those months for which

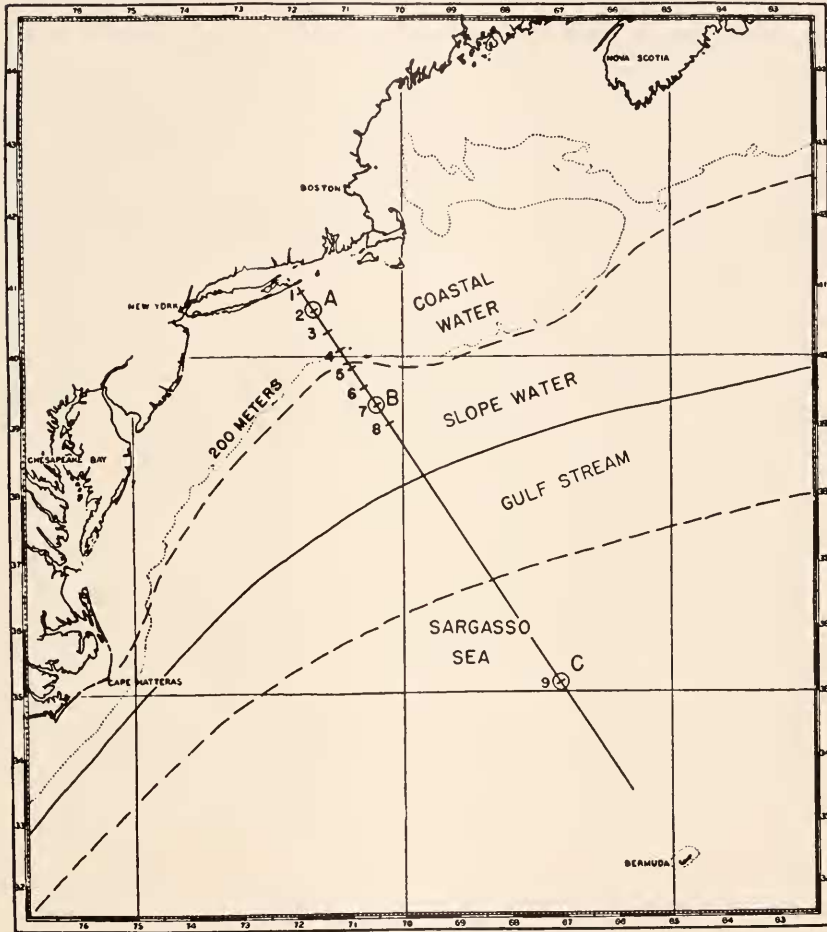


FIG. 1. The location of stations in three areas of the Atlantic. Stations 2, 7 and 9, at which certain extra observations were made, have been given the additional designation of A, B, and C respectively. The sharply delineated boundary of the Gulf Stream toward the coast is represented by a solid line; the more indefinite boundary toward Bermuda is indicated by a broken line.

we have observations in two years and also to compare our catches with those made by the U. S. Bureau of Fisheries in the coastal zone during 1929-32, which have been analyzed by Bigelow and Sears (1939).

## HYDROGRAPHY

The coastal area is distinguished from the areas farther offshore first of all by the great and important difference in the depth of the water. At Station 1 the water averaged 44 meters deep, at Station 2(A), it averaged 69 meters, and at Station 3 it averaged 85 meters. Station 4 was located just at the brink of the continental slope and the slightly different positions reached on different cruises resulted in depths which varied from 159 meters to 375 meters. The depth in the slope water area was very much greater. At Station 5, located over the steep section of the continental slope, the depth varied from 411 meters to 1,134 meters and at the other stations in this area the water was from 2,000 to 3,000 meters deep. The depth at Station 9(C) in the Sargasso Sea averaged 5,100 meters.

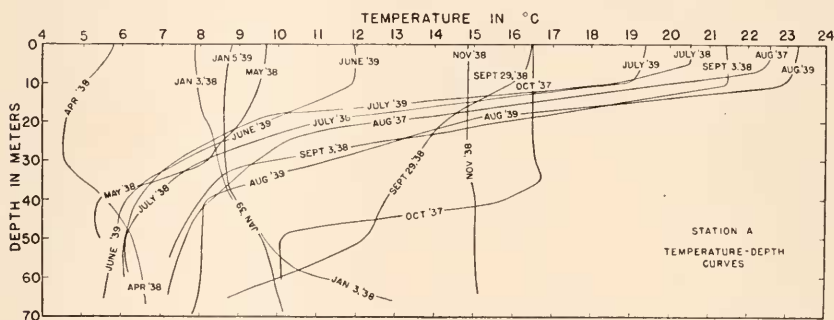


FIG. 2. *Coastal Water*—Seasonal changes in the distribution of temperature with depth at Station 2(A).

The currents in the areas under consideration are generally parallel to the coast in their broader aspect. In the coastal zone a slow and intermittent movement of the water down the coast in a southwesterly direction has been detected supplying Stations 1 to 4 with cooler and less saline water than exists offshore. In contrast, the western part of the Sargasso water, i.e., the Gulf Stream, is flowing rapidly in the opposite direction, and at Station 9(C) the highest temperatures and salinities were encountered. The slope water is an area of mixing in which intermediate conditions are to be expected. For a complete analysis of the hydrographic situation reference should be made to Iselin (1940). A synopsis of the conditions from the biological viewpoint follows.

At Station 2(A), which we may take as typical of the coastal region, the water is found to be completely mixed early in the winter with the result that the temperature is uniform from surface to bottom (Fig. 2).

Cooling continues during the winter until a minimum of about  $4^{\circ}$  C. is reached in February (Bigelow, 1933). With the arrival of the spring freshets in March and April the salinity of the surface water near the coast is reduced and consequently further vertical mixing with the deeper more saline strata tends to be resisted. At the same time the heat received from the sun, which is increasing at this season, progressively warms the water layers nearest the surface in which the major portion of the radiation is absorbed (Clarke, 1939a). Our first spring observation, in April, exhibits the beginning of the vernal warming of the uppermost layers. As this process continues on into the summer, vertical mixing is more and more retarded because of the increasing stability resulting from the greater differences between the surface and the bottom temperatures. Thus, in the late summer of our years, when the temperature at the surface reached the maximum value of about  $23^{\circ}$  C., water of only about  $8^{\circ}$  C. existed at the bottom and a sharp thermocline was to be found at mid-depths. During the autumn months cooling at the surface in combination with the stronger winds of that season results in progressively deeper stirring and the consequent further warming of the bottom layers until the winter condition of uniform temperatures is attained. The temperatures observed at Station 2(A) indicate that during the period of the present investigation the coastal water was neither abnormally warm nor abnormally cold during any season as judged by the records of previous years (Bigelow, 1933). The salinity at this station varied between  $31.20/_{00}$  and  $33.20/_{00}$  at the surface and between  $32.70/_{00}$  and  $33.90/_{00}$  at the bottom during the year. It is doubtful if these relatively slight differences in salt content are of any biological importance. The transparency of the water as measured by the percentage absorption of light per meter ranged from 10 per cent to 14 per cent (Clarke, 1939).

In the Sargasso Sea, as exemplified by Station 9(C), the depth to which the seasonal changes in temperature extend is much greater, but the range of temperature variation is much smaller than in the coastal area (Fig. 4). In the Sargasso water a "primary" thermocline extending from about 500 meters to 1100 meters is in existence throughout the year. The upper boundary of this "thermocline layer" represents the lower limit of the stirring action of the wind, and during the winter and early spring months the temperature is found to increase but little from this depth to the surface. Below 800 meters a temperature of less than  $15^{\circ}$  C. is to be found at all seasons (Iselin, 1936). In our present investigation a minimum temperature for the surface of about  $19^{\circ}$  C. was observed in April. The vernal warming which follows this winter condition not only raises progressively the temperature of the



surface, but also produces during the ensuing months a "secondary" thermocline which is found first at 40 meters but later in the summer at nearly 100 meters. This secondary thermocline disappears again during the late autumn months as a consequence of the deeper stirring of that season. During the present investigation the surface layer attained a maximum temperature of nearly  $27^{\circ}$  at the end of August. Thus, the seasonal range at the surface amounted to only 8 degrees in contrast to the 15-degree change observed at Station 2(A). The salinity in the Sargasso area is remarkably constant: in the present investigation all observations down to 300 meters were confined between 36.1 and  $36.7^0/00$ . The absorption of light by the water, which has been found

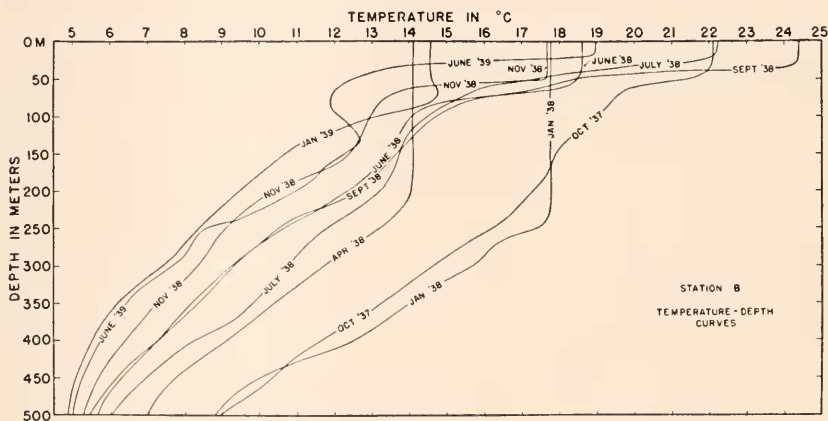


FIG. 3. *Slope Water*—Seasonal changes in the distribution of temperature with depth at Station 7(B).

to take place at an extremely low rate in this part of the ocean, varied between 4.2 per cent and 6.6 per cent per meter (Clarke, 1939a).

At Station 7(B), in the middle of the slope water zone, the hydrographic conditions were generally intermediate between those obtaining in the coastal and in the Sargasso zones. They are subject, however, to very large fluctuations, especially in the upper 200 meters, because nearly pure coastal water or nearly pure Sargasso water may be present at the station in question, and on our various visits all degrees of mixing were encountered. The seasonal temperature cycle is of the same nature here as in the Sargasso zone, but the main thermocline layer is shoaler, extending in the present case from about 250 meters to 600 meters and temperatures are generally lower (Fig. 3). Thus, at Station 7(B) the seasonal change of 10 degrees which was observed for the

surface water ranged from 14° C. to 24° C. The salinity and the transparency of the slope water similarly veer toward values characteristic of the coastal water or of the Sargasso water, according to the proportions in which those two types are present as has been discussed in detail elsewhere (Clarke, 1939a).

COLLECTION AND MEASUREMENT OF PLANKTON <sup>2</sup>

Our present plankton studies are based primarily on a pair of "oblique" hauls (one shallow and one deep) made with an open scrim

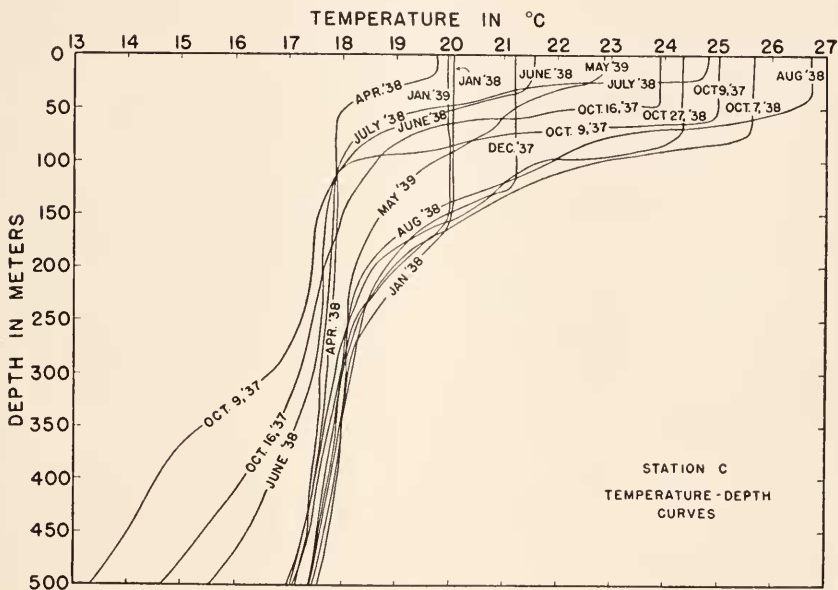


FIG. 4. *Sargasso Sea*—Seasonal changes in the distribution of temperature with depth at Station 9(C).

net (10 strands/cm.) at each of the nine stations shown in Fig. 1. For the shallow haul the net was lowered to 25 meters in most cases (but to 50 meters at Stations 7(B) and 9(C)) and hauled in at the rate of 5 meters every 5 minutes (5 meters every 2 minutes from 50-meter level), while the ship was steaming at 1½ to 2 knots. For the deep haul, the net was lowered to the bottom at Stations 1-4, to about 275 meters at Stations 5-8, and to about 800 meters at Station 9, and then, while steaming, hauled up to 25 meters (or to 50 meters) at such a rate that

<sup>2</sup> Carried out by Mr. Dean F. Bumpus, Biological Technician for the Woods Hole Oceanographic Institution.

the total towing period consumed about 30 minutes. In this way a picture was obtained of the plankton in the superficial stratum above the summer thermocline and of the plankton in the underlying strata from which some biological relationship with the surface might be expected.

At Stations *A*, *B*, and *C*, located within the three areas under consideration, additional observations were undertaken to supply further detail to the biological picture. Shallow and deep hauls with a stramin net (either 1½ or 2 meters in diameter) were made at these stations for the collection of the larger and less abundant elements of the population which might not be sampled adequately by the smaller nets. In these hauls the same depths and general procedure were used as for the work with the scrim nets. When weather permitted, both the scrim and the stramin nets were rigged for closing (Leavitt, 1935, 1938) as a check on the deductions from the open net hauls as to the exact nature of the vertical distribution of the zoöplankton. Those elements of the zoöplankton which were too small to be retained by the relatively coarse scrim net were investigated at these stations by means of shallow and deep oblique hauls with a No. 10 (43 strands/cm.) silk net 30.5 cm. in diameter. In addition, phytoplankton material was obtained at the three key stations, and in some cases at the intervening stations as well, from water samples and from hauls with No. 20 silk nets, and was turned over to Dr. Lois Lillick and to Dr. James B. Lackey for study.

For the whole of the cruise of May 29–June 5, 1938, for the major part of the cruise of July 9–17, 1938, and in certain other cases, hauls were made with plankton samplers provided with No. 10 silk nets or with No. 2 (21 strands/cm.) silk nets. The plankton sampler is a newly developed instrument consisting of a tube 12.7 cm. (5 inches) in diameter to the end of which a conical net is attached. The tube is provided with a shutter and contains a volume meter which records the amount of water which has actually passed through the net (Clarke and Bumpus, 1939). Tests reported by Winsor and Clarke (1940) indicate that a net with a diameter as small as 12.7 cm. is as reliable as a net 75 cm. in diameter. The operation of the samplers, in their earlier design, was interfered with by the unusual abundance of salpae which were encountered at a large number of the stations (see below), and it was found that the towing periods employed in the barren offshore waters were not long enough to yield a catch of satisfactory size for detailed analysis. Nevertheless, the work with the plankton samplers provides us with a certain number of cases from which the absolute density of the plankton under various circumstances can be deduced with precision. The plankton sampler hauls therefore comprise a valuable adjunct to the hauls with nets of the more usual type.

The abundance of the zoöplankton taken in the hauls has been determined in all cases by means of volume measurement and, in the case of certain species, by enumeration. The volume was measured by displacement, since Bigelow and Sears (1939) have recently called attention to the superiority of this procedure over the settlement method. The whole catch was placed in a graduated cylinder and the total volume noted. The catch was then poured through netting of the same (or of smaller) mesh than that of the net used in making the catch and allowed to stand until dripping had practically stopped. The volume of water thus separated was then measured and subtracted from the total volume to obtain the volume of the plankton alone. In those cases in which sagittae, salpae, or coelenterates formed an important fraction of the total catch, these elements were picked out and measured separately. The remaining plankton, composed chiefly of copepods and euphausiids but containing also some amphipods, limacina, etc., has been designated as the "crustacean" fraction of the haul.

The species in the present study which were enumerated were the important copepods, *Calanus finmarchicus* and *Centropages typicus*. Separate count was kept of the males and females and, in the case of *Calanus*, of the developmental stages as well. The method employed for sub-sampling and for counting<sup>3</sup> was that described by Winsor and Clarke (1940).

#### VARIABILITY IN VOLUME AND IN TYPE OF PLANKTON

The volumes of all the hauls made with the scrim net in the present investigation are presented in Tables I and II, which give respectively the values for the "total plankton" and for the "crustacean plankton." It will be observed that the amounts of plankton caught are extremely variable, ranging from a maximum of 3,060 cc. to a minimum of 1 cc. in the case of the total plankton and from 225 cc. to 1 cc. for the crustacean plankton. Very considerable changes in volume were often encountered at neighboring stations, as was also observed by Bigelow and Sears (1939). This situation immediately raises the question of the reliability of single hauls. Fortunately there is available a statistical study of the variation to be expected from just such material as is dealt with here in the report of Winsor and Clarke (1940). These investigators found that in the case of oblique hauls with a 75 cm. scrim net, the standard deviation of the haul-to-haul variation was about 20 per cent of the mean. It is therefore obvious that the major portion, at

<sup>3</sup> Several small hand "counting machines" mounted on a board were found to be extremely useful for keeping count of the various categories observed through the microscope.





TABLE II

Crustacean plankton. Volume in cc. of plankton after removal of major portion of sagittae, salpae and coelenterates taken with 75 cm. scrim net. Volume reduced to 30-minute haul. Hauls in italics taken between sunset and sunrise. S = shallow, D = deep (see text).

Station	Depth	1938 Jan. 2-7	1939 Jan. 3-10	1938 Apr. 6-13	1939 May 28-June 3	1938 July 9-17	1938 Aug. 28-Sept. 3	1938 Sept. 29-Oct. 8	1937 Oct. 2-9	1937 Oct. 17-21	1938 Oct. 27-Nov. 3	Average
Coastal Water	1	26	—	—	62	37	8	—	38	20	56	
	D	20*	—	—	64	71	—	—	126	27	60	
	S	20*	—	15	84	91*	52	14	46*	—	50	
	S	20*	—	4	54	214	156	—	62*	—	48	
Coastal Water	3	24	4	1	162	—	45	0	85	—	74	
	S	20	7	—	126	68	47	22	86	—	62	
	D	20	—	84	11	—	17	10	25	—	70	
	S	—	—	—	73	—	135	22	103	—	16	
Coastal Water	Average	23	4	33	80	64	60	12	48	20	62	41
	Deep	18	7	33	79	118	143	22	94	27	50	
	Shallow	18	—	—	—	—	—	—	—	—	—	
	Combined	19	6	11	79	104	122	19	82	25	47	50
Slope Water	5	2	18	8	9	—	—	—	21	—	—	
	S	10	40	40	11	—	—	—	12	—	—	
	D	16	9	17	15	—	—	12	45	—	4	
	S	8	11	32	18	—	1	7	39	—	11	
	S	5	11	32	79*	—	16	14*	45	4	68*	
	S	25	25	8	48*	—	3	10*	23	12	16*	
	D	7	28	8	1	—	14*	9	15	—	14	
	S	7	28	8	1	—	76	—	20	—	15	
Slope Water	Average	10	17	15	22	—	27	12	32	4	18	
	Deep	8	33	24	22	—	15	9	24	12	14	
	Shallow	8	—	—	—	—	—	—	—	—	—	
	Combined	9	32	23	22	—	16	9	25	11	15	
Sargasso Sea	9(C)	29*	5	19*	10	—	6	16	44	5	21	17
	50-0 m.	—	10	49*	16	—	24	19	—	4	6	17
	100-500	—	13	5	—	—	4	5	6	3	2	5
	500-5000 (Weighted)	4	12	4	—	—	7	—	—	4	4	3
Combined	5	12	7	13	—	—	4	—	10	4	7	

\* Occasions on which the small copepods in the corresponding No. 10 silk net haul amounted to > 5 cc.



least, of the fluctuation in volume observed in the present case is real and not due to errors of observation.

A further question, and one more difficult to answer, is the extent of the area over which each haul may be taken as representative. Previous plankton studies have shown that the dispersal pattern of the population in each situation must be investigated individually. For this pur-

TABLE III

Comparison of three sets of 30-minute hauls with 75 cm. scrim net at Station 2(A) as a sample of variability.

	Oct. 2, 1937 Closing net (Day Haul)	Oct. 2, 1937 Open net (Day Haul)	Oct. 3, 1937 Open net (Night Haul)
Total volume (cc.)			
Shallow	33	140	45
Deep	46	127	150
Total	79	267	195
Crustacean volume (cc.)			
Shallow	33	14	38
Deep	46	58	126
Total	79	72	164
Calanus stage IV			
Shallow	250	234	400
Deep	1,940	3,000	6,500
Calanus stage V			
Shallow	500	117	900
Deep	2,500	7,200	16,200
Centropages ♂			
Shallow	8,500	5,050	5,800
Deep	21,600	24,600	15,500
Centropages ♀			
Shallow	22,200	9,800	14,800
Deep	51,000	41,100	28,500

pose a closer network of stations must be arranged than was possible in the present case and strictly quantitative hauls employed, as, for example, through the use of registering plankton samplers (Clarke and Bumpus, 1939) or of a continuous plankton recorder (Hardy, 1936).

In the present investigation two bits of evidence exist on the variability of hauls closely spaced in time and in position. At Station 2(A) on October 2, 1937, a pair of hauls with the closing scrim net was followed immediately with a pair of hauls of the same type with the open

net and in addition the open net hauls were repeated at this station on the following day (Table III). In each of the categories compared in this table, the largest volumes are found to be three or four times greater than the smallest volumes. In those cases in which numbers of individuals are compared, the differences are greater. Evidently the variations of the separate groups considered tend to cancel out when volumes of mixed species are compared.

A more extensive study of the variation encountered within a small area was made on May 17-18, 1938, when hauls were made with the scrim net and with the plankton samplers (No. 2 silk) at Station 2(A) and at four stations located about 10-15 miles distant to the south, east, north, and west respectively of Station 2(A). The work with the plankton samplers was repeated at Station 2(A) on May 30, 1938. The variation in the volumes of these hauls and in the number of *Calanus* in copepodid stages IV and V may be observed in Table IV. Not only did the volumes fluctuate irregularly from station to station with differences as great as 10-fold in extreme cases, but also it is seen that the variations in the shallow stratum did not conform to those in the deeper layers. As in the previous case, the fluctuations in the actual numbers of *Calanus* are even greater than the changes in volume. The histogram plots of Figs. 5 and 6 reveal the very great extent to which the species composition of these hauls varies. The diagrams show, for example, that at some of the stations in this group *Calanus* was the dominant form in the catches of the scrim net, whereas at other stations small medusa were by far the most abundant organisms. Similarly, in the case of the hauls with the plankton samplers, the proportion in which each type of animal is represented varies tremendously—in one haul *Calanus* takes the lead, in other hauls *Evadne*, *Pseudocalanus*, or medusae greatly outnumber all the other forms.<sup>4</sup> In view of this far-reaching irregularity in distribution, it is essential that the number of stations occupied be as large as possible and that all hauls within each area be combined in suitable ways before any conclusions be attempted in regard to relative richness. In the following discussions, therefore, *average values* will be considered for the most part for each of the areas under consideration.

In all the foregoing data it is evident that the variability of "crustacean volume" is much less than that of the "total volume." We may conclude, therefore, that fluctuation in the abundance of salpae, sagittae, coelenterates and other non-crustacean elements are largely responsible for the great irregularities of Table I. The more uniform complexion of the hauls during the winter months is largely due to the fact that the

<sup>4</sup> The dominant species were not expected to be the same as in the scrim net hauls since the netting in the plankton samplers was of smaller mesh.

TABLE IV

Comparison of scrim net hauls at Station 2(A) and at four surrounding stations 10-15 miles distant on May 17-18, 1938, and comparison of plankton sampler hauls for the same stations and for Station 2(A) on May 30, 1938.

	Scrim net (75 cm. diameter). Vol. or no. per 30 min. haul						Plankton sampler. Vol. or no. per m <sup>3</sup> . of sea water					
	Sta. 2(A) May 17, '38 (Day Haul)	Sta. 2(A)-S May 17, '38 (Night Haul)	Sta. 2(A)-E May 18, '38 (Night Haul)	Sta. 2(A)-N May 18, '38 (Day Haul)	Sta. 2(A)-W May 18, '38 (Day Haul)	Sta. 2(A) May 17, '38 (Day Haul)	Sta. 2(A)-S May 17, '38 (Night Haul)	Sta. 2(A)-E May 18, '38 (Night Haul)	Sta. 2(A)-N May 18, '38 (Day Haul)	Sta. 2(A)-W May 18, '38 (Day Haul)	Sta. 2(A) May 30, '38 (Night Haul)	
Total volume (cc.)	57	119	23	112	75	1.02	.94	.31	.71	.76	.34	
Shallow*						.48	.56	1.08	.29	.74	—	
Intermediate †	21	120	112	13	26	1.90	.90	.96	1.02	1.15	—	
Deep ‡						—	—	—	—	—	—	
Crustacean volume (cc.)	57	119	18	28	8	—	—	—	—	—	—	
Shallow												
Intermediate	21	105	25	11	26	—	—	—	—	—	—	
Deep												
Calanus stage IV	31,500	29,400	7,550	12,700	1,900	785	161	202	475	310	87	
Shallow						84	218	111	100	167	32	
Intermediate	4,950	26,700	7,500	1,940	2,420	69	27	218	101	96	66	
Deep												
Calanus stage V	16,300	22,200	4,580	7,750	2,050	108	75	24	35	38	73	
Shallow						42	175	174	44	53	45	
Intermediate	6,400	32,800	10,500	4,750	5,500	57	113	115	82	32	10	
Deep												

\* "Shallow" for both scrim net and plankton sampler indicates oblique haul from 25 meters (wire out) to surface.

† "Deep" for scrim net indicates oblique haul from bottom to 25 meters; for plankton sampler, bottom to 50 meters.

‡ "Intermediate" for plankton sampler indicates oblique haul from 50 meters to 25 meters.

plankton at that season consisted mainly of crustacea, particularly at stations toward the coast. Salpae, which were unusually abundant during the present investigation, not only in the slope water, where they are known to be common, but also in the coastal water, most frequently accounted for the difference between the crustacean volume and the total

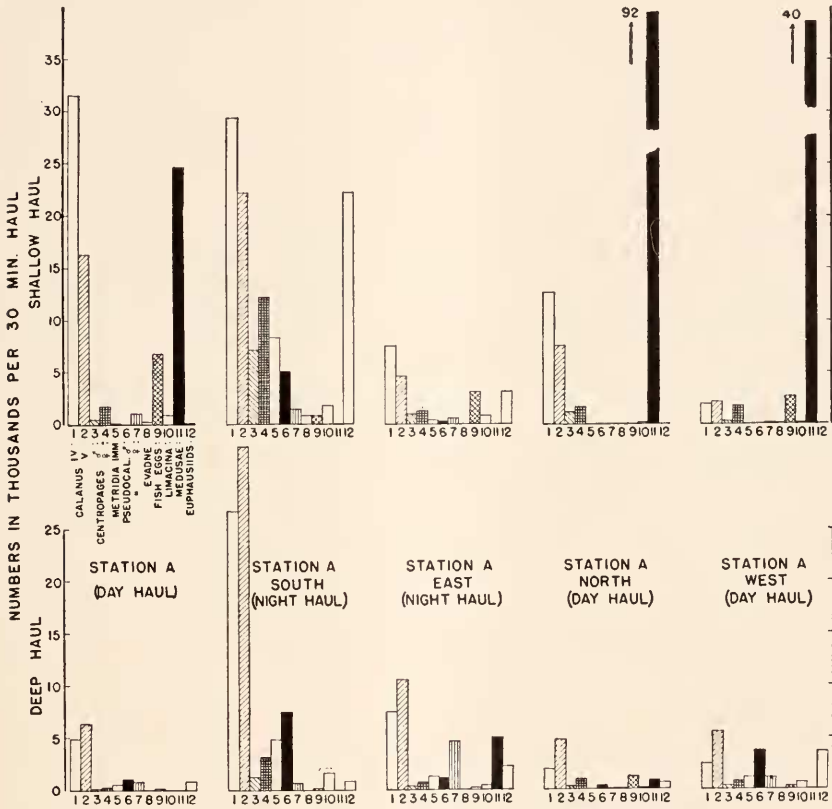


FIG. 5. Variation in composition of scrim net hauls at Station 2(A) and at four surrounding stations 10-15 miles distant on May 17-18, 1938.

volume. Indeed, in every case but one, values greater than 200 cc. were attributable to the presence of salpae.

The separation of the crustacea from the other types of animals provides us with an approximate division of the plankton into (1) the "more nutritive" forms which are known to be prominent in the diet of the important fish of the region and (2) the forms of little or no nutritional value. This method of subdivision conforms to that adopted by Bigelow and Sears (1939) with the exception that these authors

included the sagittae with the crustacea as being of considerable food value. Since in the present investigation sagittae were relatively rare (occurring chiefly in the winter months) and in no case amounted to more than 50 cc., it appears legitimate in this case to regard our "crustacean volumes" as comparable to the category of "more nutritive forms" dealt with by Bigelow and Sears. The volumes appearing as "crustacean plankton" (Table II) may thus be accepted as a rough index of

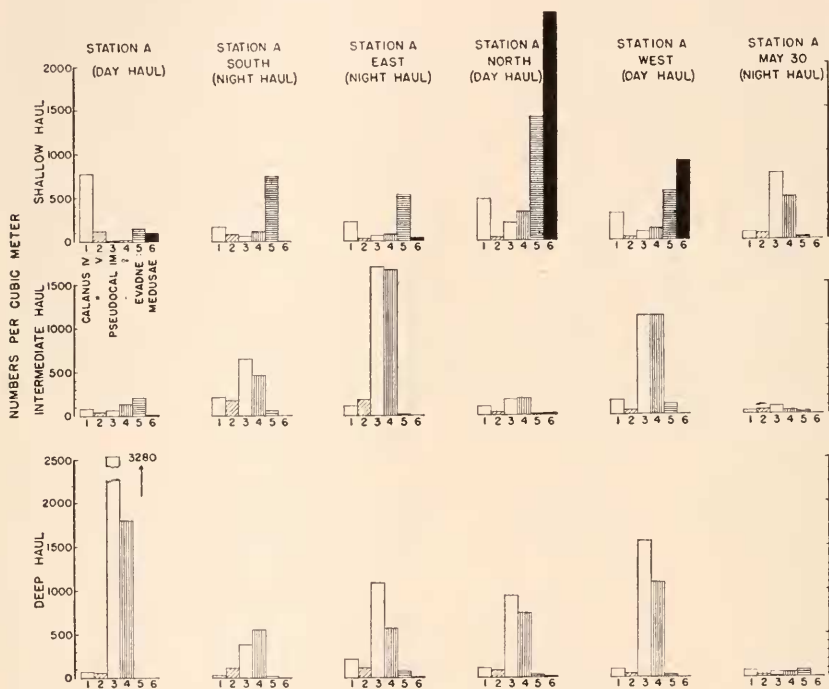


FIG. 6. Variation in composition of plankton sampler hauls at Station 2(A) and at four surrounding stations 10-15 miles distant on May 17-18, 1938 and at Station 2(A) on May 30, 1938.

the abundance of food for plankton-feeding fish within the bounds of the present investigation.

Hauls made with the large stramin nets and with smaller nets of No. 10 silk at Stations *A*, *B* and *C* were examined for the possible occurrence of important elements of the plankton which were either too large and active or too small to be caught adequately by the scrim nets. The volumes of plankton taken by the stramin nets were of the same order of magnitude as those taken by the scrim nets although the amount of water

filtered by the former type of net was very much greater. Evidently the loss of the types of plankton which slip through the meshes of the stramin net is relatively greater than the additional number of active species which are taken by this net but missed by the scrim net. A certain portion of larger crustacea were found in the stramin net hauls but the bulk of the more voluminous catches consisted of salpae, as was the case with the scrim net hauls. At the other end of the size scale there exist members of the plankton community which are not retained even by the scrim net. Hauls made simultaneously with scrim and with fine silk nets of the same size (unpublished records) have shown that in situations where small copepods (such as *Pseudocalanus*, *Paracalanus*, or immature *Centropages*) are abundant, the catch of the silk net may be several times greater than that of the scrim net. Under such circumstances the volumes of scrim net hauls alone would greatly underrate the richness of the plankton. However, the hauls with the No. 10 silk nets indicate that the smaller animals were not generally abundant during the present investigation. Amounts of crustacean plankton greater than 5 cc. were taken in these nets on only three occasions at Station *A*, four occasions at Station *B*, and two occasions at Station *C*, as indicated in Table II. Volumes greater than 10 cc. were taken only at Station *A*, once in July and once in October. We may conclude, therefore, that for the investigation as a whole the scrim net sampled the major portion of the population and that the hauls with this net are a satisfactory index to the richness of the animal plankton.

#### DISTRIBUTION OF PLANKTON BY VOLUME

##### *Vertical Distribution*

The vertical distribution of the plankton in the three areas may be ascertained from Tables I and II, in which the volumes taken in the "shallow" and "deep" hauls at each station are compared. Since the time of visiting each station fell at various hours of the day or night, the influence of any diurnal vertical migrations on the picture presented must be considered (Clarke, 1933 and 1934). For this purpose the hauls made during the day between sunrise and sunset have been differentiated in the tables from those made during the night.

For the total plankton in the coastal area, the deep hauls were greater than the surface hauls in 62 per cent of the stations occupied during daylight hours and in 67 per cent of the night stations. In the slope water area the deep hauls were greater in 58 per cent of the day stations and in 54 per cent of the night stations. These figures indicate that the vertical distribution of the plankton as a whole is essentially the same by day or



by night in these areas. When the crustacean plankton is considered separately, it is found that in the coastal area the deep hauls were greater than the surface hauls in 75 per cent of the day hauls and in 60 per cent of the night hauls. In the slope water area the deep hauls were greater in 100 per cent of the day hauls but in only 42 per cent of the hauls made during the night. These figures make it clear that a diurnal vertical movement of the crustacea was taking place in the slope water area and to a lesser extent in the coastal water. Unfortunately, all the hauls except two at Station 9(C) in the Sargasso Sea fell during the night period and consequently we are unable to state whether the distributional picture would have been different had a significant number of day hauls been made (cf. Waterman, Nunnemacher, Chace, and Clarke, 1939).

For a *general* consideration of vertical distribution in the coastal area the day and night hauls may be averaged since the differences between them are not great. The average volume of the total plankton of all the shallow hauls in this area was 118 cc. and of the deep hauls was 220 cc. If, however, the cruise of July 9-17, 1938 is omitted because of the presence in one haul of an exceptionally large number of salpae, these values become 120 cc. for the surface and 119 cc. for the deep hauls. The average volumes of the crustacean plankton in this area were 41 cc. for the shallow hauls and 50 cc. for the deep. In the slope water area day and night hauls may similarly be averaged for a general consideration since there are an equal number of each. In this area the total plankton averaged 77 cc. for the shallow hauls and 50 cc. for the deep hauls and the crustacean plankton averaged 18 cc. for the hauls at both levels. We may therefore conclude that for the year as a whole no important difference existed in the richness of the plankton in the upper and lower strata in these two areas. At the station in the Sargasso Sea, the volume of the crustacean plankton and of the total plankton was about the same in the uppermost 50 meters of water as it was in the stratum from 100 meters to 40 meters. But in every case except one (in which the shallower hauls were made during the day) the plankton was more abundant above 100 meters than in the deeper strata.

#### *Seasonal Distribution*

In order to obtain a value characteristic of the whole population in each area for each season and to eliminate any localized influence which diurnal migration might have on the distributional picture, we may combine the shallow and deep hauls for each of the cruises. It must be remembered, however, that at no station was it practicable to allow the net to fish down to the very bottom and at the deeper stations a considerable

stratum remained unsampled. Although the possibility exists that a population of some importance might thus have been missed, we have no evidence that the plankton just over the bottom on the continental shelf is significantly more abundant than in the water nearer the surface. In the oceanic areas with which we are concerned here, Leavitt (1938) found that the macrozoöplankton was considerably less rich below 1,000 meters than above that depth. In combining the average hauls at the two levels, the deep haul has been weighted in proportion to the relative thickness of the stratum through which it was towed as compared with the shallow haul. The combined average is thus a characteristic index of the whole depth of water sampled.

Considering first the coastal area, we find that the plankton as a whole reached its lowest ebb during the winter in both 1938 and 1939 (Table I). By the end of May, the volume of the catches was greatly increased and in July and August the plankton bulked twenty to forty times as large as it did in the winter, the augmentation being most pronounced toward the outer edge of the continental shelf where the salpae were especially abundant. Early in October the haul volumes were of about the same size as in May, but a decline appeared by the middle of October in 1937 and at the end of that month in 1938 and the population presumably continued to shrink until the following January. The magnitude of this seasonal increase in volume appears to be considerably greater than that reported by Bigelow and Sears (1939) for even their best plankton years, but the contrast is largely due to the fact that our values at the beginning of the year are lower. Our summer volumes generally did not attain the size of those found by the earlier workers. In the present investigation the volumes of the crustacean plankton (Table II) followed much the same course as did the total plankton, since smallest values were taken in the winter and largest values during July and August. It is of interest to note that the crustacean element was still at a low ebb in April, and that in 1938 a period of scarcity occurred early in October followed by increased volumes at the end of the month, whereas in 1937 no prominent decline occurred until the middle of October.

In the slope water area little, if any, information existed previously on seasonal variation in richness. From our present data we may observe that although the average values for the total plankton did not vary over as great a range as was the case in the coastal area, and although the fluctuations were irregular, nevertheless, the hauls of smallest volume occurred during the colder part of the year and values as much as ten times greater were found in May and October. In the case of the crustacean plankton, however, the largest volume of the year was less than four times the smallest volume and both high and low values oc-

curred at all seasons. Cognizance should also be taken of the fact that the average volumes of both the total plankton and of the crustacea differed widely in January, 1938 from those found in January, 1939 and a similar lack of agreement occurred between the values of early October, 1937 and 1938.

At our station in the Sargasso Sea there is even less evidence of a seasonal fluctuation in the richness of the plankton. As far as the total plankton is concerned, the largest average volumes were obtained in January, 1939, in April and in May-June, but volumes of almost equal magnitude were taken in September and October. Furthermore, since the individual hauls vary so greatly in size, we probably would not be justified in designating any one season as a period of increased plankton abundance. The same conclusion applies to the crustacea since the volume of this fraction of the plankton also varied irregularly, and since the highest value recorded was only about four times the lowest. It thus appears that among the three areas investigated indication of a significant seasonal change in richness for the total plankton was found only in the coastal and slope water zones and for the crustacean plankton only in the coastal area. Especially noteworthy was the occurrence of seasonal differences of greater magnitude than was suspected heretofore.

#### *Regional Distribution*

If the plankton volumes for all seasons are now combined, a basis is formed upon which a rough quantitative comparison may be made for the first time of the average differences in the richness of the several areas. This operation yields a grand average of 194 cc. for the volume of the zoöplankton of all types taken with the 75 cm. scrim net in the standard 30-minute haul in the coastal area. This figure is nearly four times as great as the average value of 52 cc. for the slope water area, which in turn is about four times the magnitude of the grand average of 12 cc. for our station in the Sargasso Sea (Table I). The average volumes for the crustacean plankton were 50 cc., 18 cc., and 7 cc. for the coastal area, the slope water area and the Sargasso Sea respectively (Table II). The abundance of the crustacea thus exhibited the same downward trend in passing offshore as was observed for the total plankton although the differences were only 2 or 3-fold in this case. Since we cannot yet make an adequate statement concerning the growth rate of the animals considered here, or rate of replenishment of the populations, no general conclusion can be drawn concerning the "productivity" of these areas in a broader sense. However, the present investigation does clearly indicate the existence in the coastal area of a "standing

crop" which, on the average, significantly exceeds that characterizing the water farther offshore.

#### VARIATION IN ABUNDANCE OF CALANUS AND CENTROPAGES

The foregoing study of the variations in volume of plankton in the three oceanic areas under consideration has been supplemented by a numerical analysis of the fluctuations in two individual species of prominence—the copepods, *Calanus finmarchicus* and *Centropages typicus*. The variations in the abundance of *Calanus* are presented graphically in Fig. 7, where all stages which were caught by the net (copepodid stages IV and V and adults) have been added together and the shallow haul and deep haul (weighted) have been combined for each station.

It is clear from the graph that by far the major portion of the *Calanus* population is to be found in the coastal area, although a small number of this species was taken at Stations 6 and 7. No *Calanus finmarchicus* were found at Station 9 in the Sargasso Sea. The fact that the richest hauls were made at Stations 2, 3 and 4 with only moderate numbers at Station 1 is consistent with the distributional picture for this species presented by Bigelow and Sears (1939, Fig. 23). *Calanus* reached its greatest abundance during April, June, and July in the present survey as was also the case for the average of the years 1929–32 in the northern half of the area studied by Bigelow and Sears. At the station in the western entrance to Vineyard Sound occupied by Clarke and Zinn (1937), *Calanus* was similarly found to be most numerous from April to August. It therefore seems well established that the spring and summer months are the seasons at which *Calanus* comes into prominence as a member of the plankton community in this region.

The subdivision of the *Calanus* population into its sex and age groups at the stations in the coastal area throughout the year may be scrutinized in Fig. 8. The histograms here presented show that the great variability which characterized both the volumes and the species composition of the hauls also extends to the subdivisions within a single type of animal. Not only do the sex and age groups differ among the several stations on the same cruise, but in addition we find variations from year to year. Nevertheless, certain generalities appear. Copepodid stage V was the most numerous group for the investigation as a whole and particularly so during the autumn and winter months, but stage IV became prominent in May and June and in September. The occurrence of the adult females, which were the next most abundant, was rather irregular although there was some indication that this group was more usual near shore than at Stations 3 and 4. The fact that out of the total number

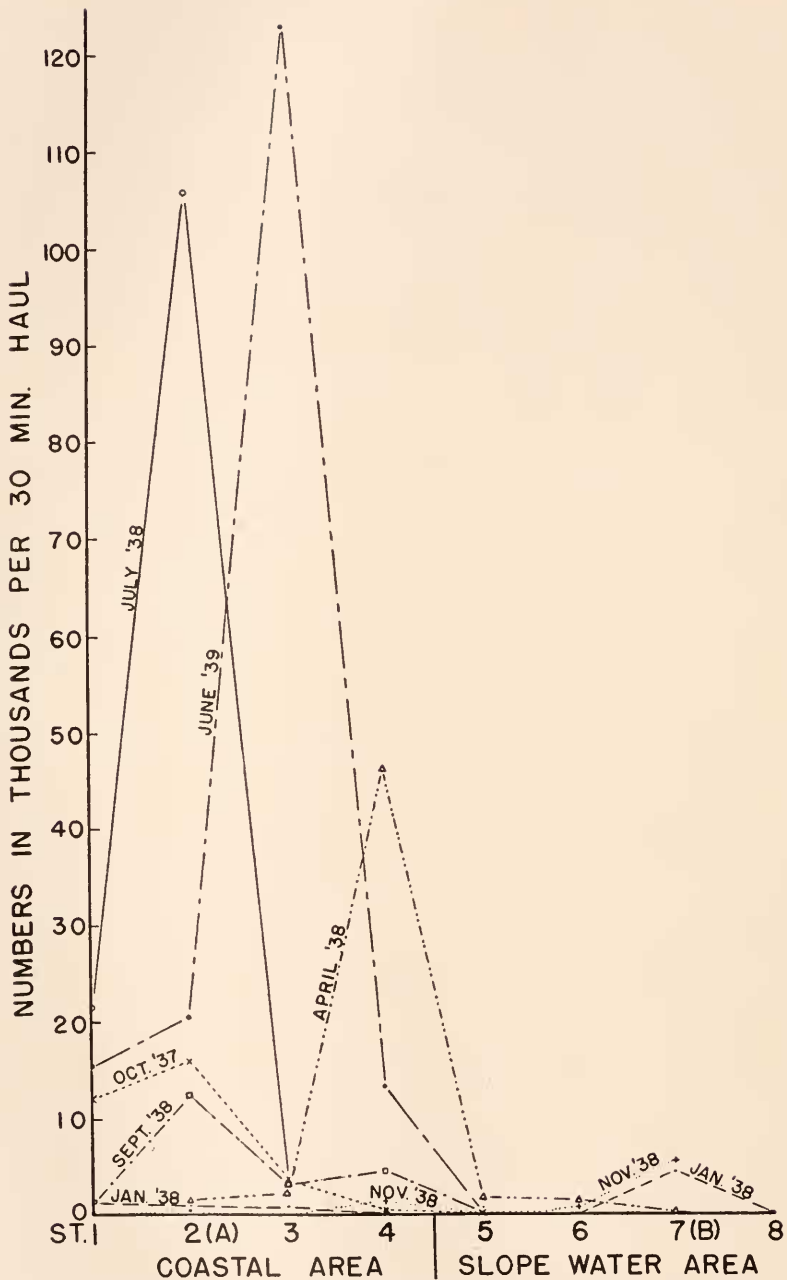


FIG. 7. Variation in abundance of *Calanus finmarchicus* (all stages) throughout the year. Shallow haul and deep haul (weighted) have been combined. Numbers of animals on cruise of Sept. 29–Oct. 2, 1938, too low to appear in graph. On cruise of Jan. 5–9, 1939, *Calanus* taken at Station 5 only.

of hauls adult males of *Calanus* were found only in January and in May and June agrees very closely with the observations at the station occupied several years earlier by Clarke and Zinn (1937). These investi-

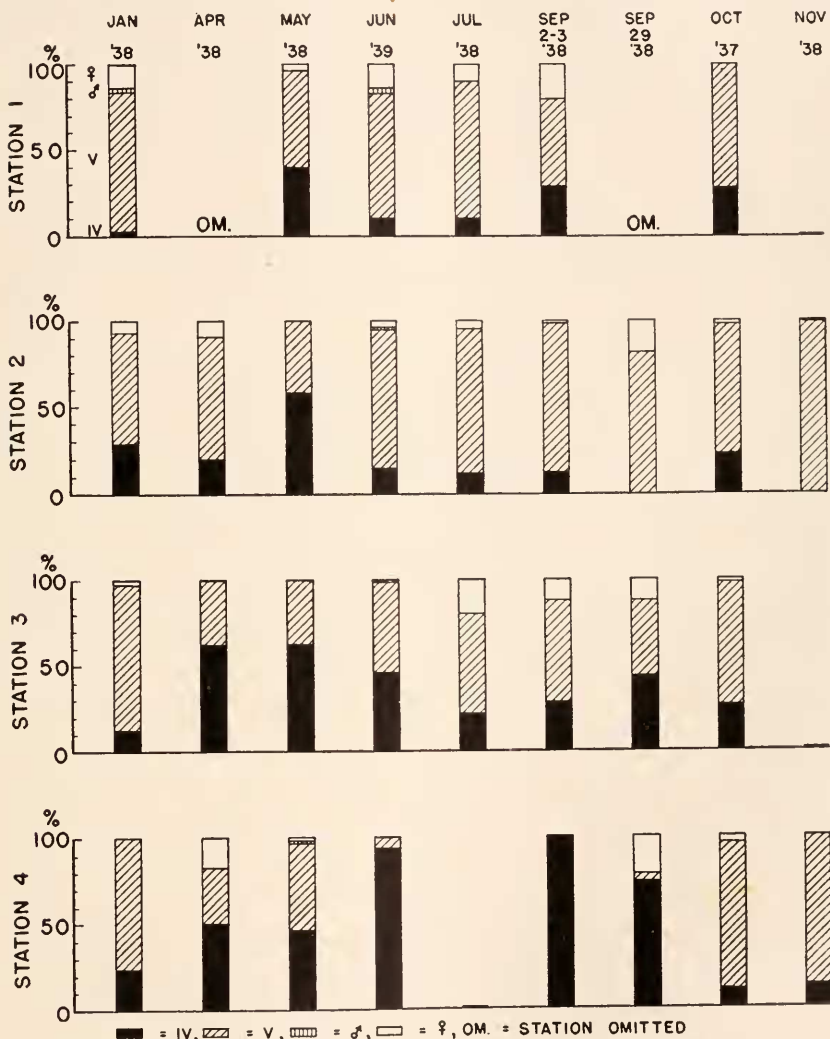


FIG. 8. Percentage age and sex distribution of *Calanus finmarchicus* throughout the year (coastal area only). On cruise of Jan. 5-9, 1939, no *Calanus* taken in this area.

gators reported that *Calanus* had two breeding periods during the year, one resulting in a short-lived spring generation,<sup>5</sup> and the other in a long-

<sup>5</sup> The conclusions of Clarke and Zinn (1937) have been erroneously stated by Bigelow and Sears as "two shorter-lived generations during the spring, followed by a longer one in summer."



lived generation spanning the balance of the year. They also found that the appearance of the adult males presaged the commencement of breed-

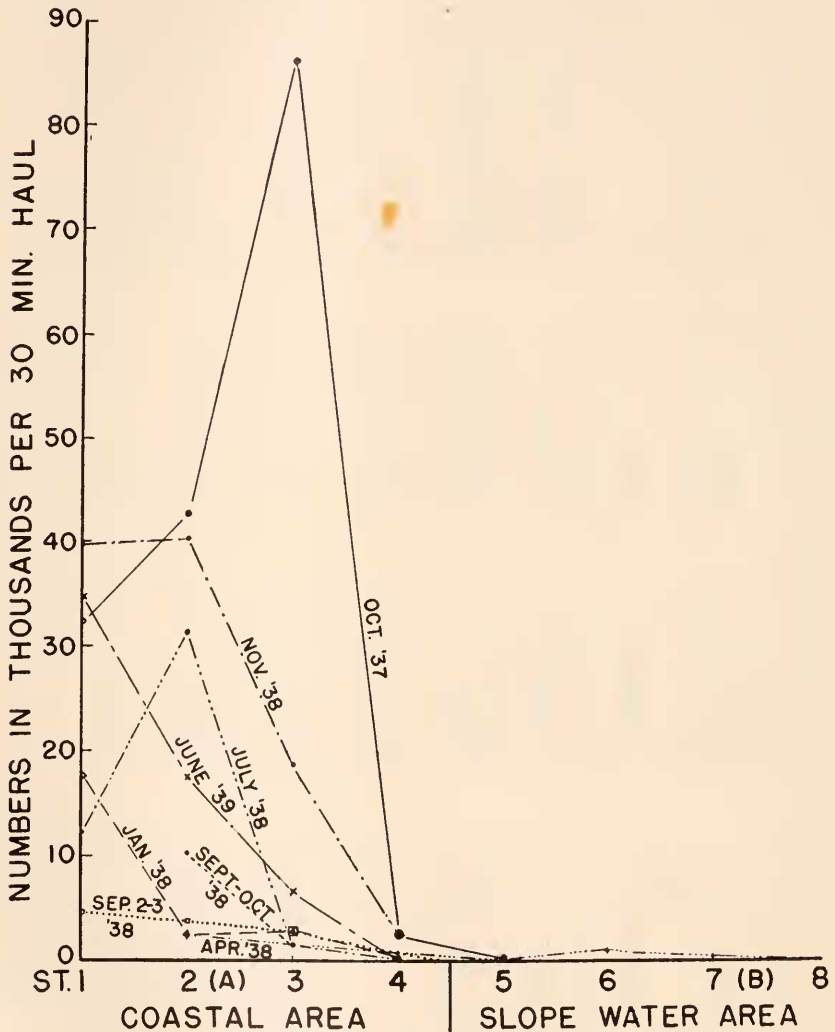


FIG. 9. Variation in abundance of *Centropages typicus* (all stages) throughout the year. Shallow haul and deep haul (weighted) at each station have been combined. On cruise of Jan. 5-9, 1939, *Centropages* taken at Station 3 only.

ing activity in this species. Consequently, the deduction seems justified that two generations of *Calanus* similarly occur each year over the whole of that part of the coastal area covered by the present investigation.

The horizontal distribution and seasonal changes in *Centropages typicus* are similarly presented in Fig. 9, in which the numbers of adult males and females and of immature specimens have been added together, and shallow and deep hauls combined. The graph shows that this species

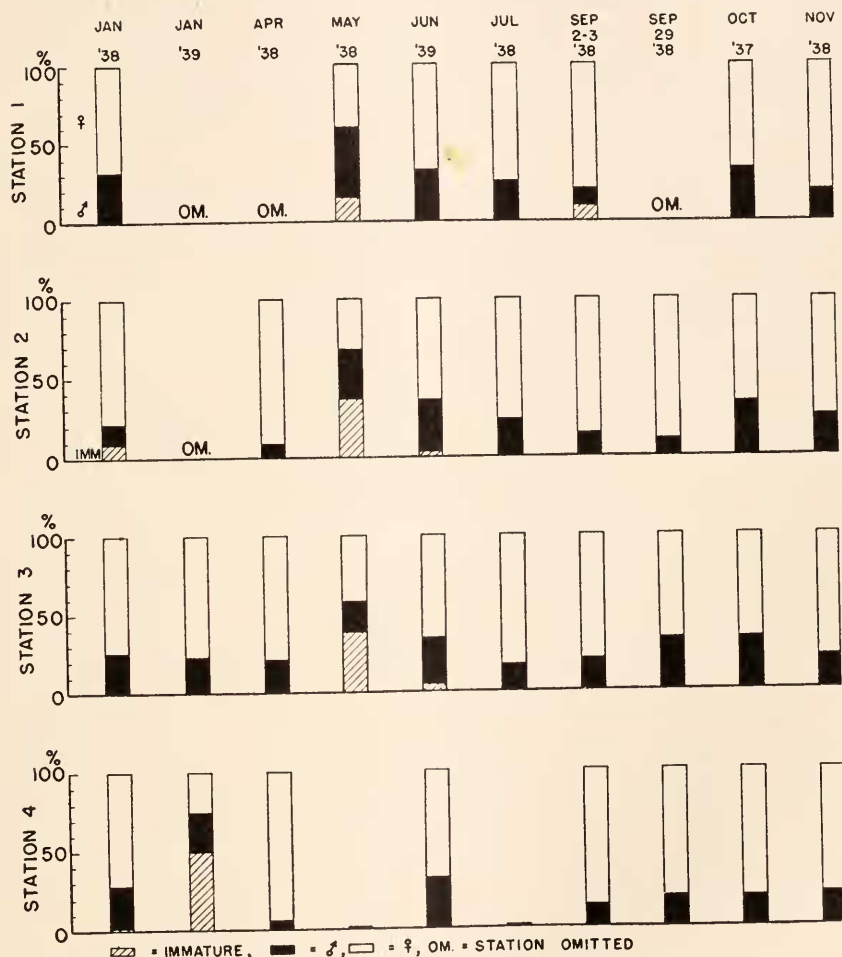


FIG. 10. Percentage age and sex distribution of *Centropages typicus* throughout the year. (Coastal area only.)

is restricted to the coastal area even more completely than was *Calanus*. Moreover, *Centropages* was never really abundant at the outer edge of this area (Station 4) and large numbers were frequently encountered near shore (Station 1). The population of this copepod was generally at a low ebb during the winter and spring months, but catches of greatly

increased size were taken from June to November. The largest hauls of the series were made early in October, 1937 but numbers were relatively small during the same period in 1938, although sizeable catches were taken in November of that year. Yet, in spite of the fact that great irregularity is encountered here as elsewhere, we may conclude that in general *Centropages* reaches its peak of abundance during the summer at a period somewhat later than that typical for *Calanus*, and that it may continue to be plentiful well into the autumn. Our data, therefore, confirm the earlier deductions of Clarke and Zinn (1937) and of Bigelow and Sears (1939).

Both male and female adults of *Centropages* were well represented in our catches in the coastal area throughout the year in contrast to the situation with *Calanus* (Fig. 10). The females were more numerous than the males in almost every case but the males most nearly reached parity in May and June and again in September and October. The immature specimens were probably not taken in their true proportions by the relatively coarse scrim net, but if abundant in the water, they were represented qualitatively in the catches. A considerable percentage of immature *Centropages* was taken by the plankton samplers with No. 2 silk mesh in May, 1938 and by the scrim nets in January, 1939. Occurrences of smaller proportions were observed in January, 1938, June, 1939 and September, 1938. Clarke and Zinn (1937) report the immature stages of this copepod to have been particularly abundant in the summer months at their station. Bigelow and Sears (1939), however, did not distinguish between the immature and the adult specimens of this species. Our information is thus too scanty to determine the time of breeding for *Centropages*, but the fact that young individuals were encountered at every season except the autumn strongly suggests that more than one breeding period and probably more than one generation occur during each year. However, since the majority of *Centropages* evidently do not pass the autumn and winter in a late copepodid stage, it appears probable that the life cycle of this species differs markedly from that of *Calanus*.

#### DISCUSSION

The first impression which we derive from the foregoing data is one of variability. We have found that plankton hauls repeated within a short period at the same station or at nearby positions differed widely not only as to total quantity but also as to composition. Furthermore, from season to season the plankton oscillated with an amplitude which varied according to the location and which in certain cases was as great

as 20- to 40-fold. In addition, both the type of plankton and its abundance in any area were found to differ in the same month according to the year. It appears, then, that any plankton study in an oceanic region of this type must be prepared to deal with time and space fluctuations on both a small and a large scale. This investigation has shown that no single station will serve as an adequate index for any of the areas under present consideration—a conclusion which was suspected from plankton work elsewhere. Also, it has become clear that a network of stations repeated throughout the year for several years will be necessary before the causes underlying these fluctuations can be ascertained.

As a step in this direction, the findings of the present investigation may be compared with and added to the results of the earlier explorations in these waters which have been thoroughly analyzed by Bigelow and Sears (1939). Unfortunately almost all the quantitative plankton work in this part of the Atlantic has been confined to the waters overlying the continental shelf. The whole of the area dealt with by Bigelow and Sears corresponds to only one of the zones crossed by our cruises—namely the coastal area. Nevertheless, since this region is the most changeable and also the most important from the point of view of the commercial fisheries, a comparison is highly desirable.

The location of the "Montauk Section," as designated by Bigelow and Sears, corresponds most closely to the position of our Stations 1 to 4. The volume of the total zoöplankton taken at stations on the Montauk Section during the years 1929–32 ranged from 3 to 1,880 cc., but out of a total of about 60 hauls only five hauls were less than 100 cc. and 17 hauls were greater than 500 cc. in volume. These figures contrast rather sharply with those obtained in the present investigation. Among our 58 hauls in the coastal area only 5 were more voluminous than 500 cc. and 31 contained less than 100 cc. The volumes of hauls in the present survey were generally inferior even to those of the years 1929 and 1932 which were reported to be years of plankton scarcity. The discrepancy may be explained to some extent by the difference in the type of net employed, for the plankton measured by Bigelow and Sears was taken with a net 1 meter in diameter, the top of which was made of No. 0 silk (15 strands/cm.) and the tail of No. 2 silk (21 strands/cm.). In addition to the fact that this finer mesh silk would tend to catch more of the smaller organisms than the scrim employed by us, it may well be that the filtering efficiency of the silk is superior to that of the scrim, which was estimated by Clarke and Zinn (1937) to be as low as 20 per cent. However, the effect of the larger net and finer mesh is offset to some extent by the fact that Bigelow and Sears reduced their data to a standard haul of 20 minutes instead of the 30 minutes

employed in the present study. The combined effect of the differences in net size and in duration of haul would yield a theoretical factor of .84 to be applied to the volumes reported by the earlier workers, but the allowance which should be made for other differences in method is not known. Although the discrepancy is very likely not as great as would at first appear, nevertheless, everything considered, it seems probable that the plankton was really less abundant during the period of the present survey than it was during any of the years 1929-32.

A much more precise measure of the actual abundance of the plankton may be obtained from the hauls made with the 5-inch plankton samplers since these instruments are equipped with calibrated flow meters. Unfortunately, the samplers were not developed early enough to be used for the whole investigation, but it is of some value to examine such hauls as we have for their order of magnitude. Although the samplers are extremely useful in coastal regions, they are less satisfactory (in their present design) for work in the areas farther offshore since the scarcity of the plankton causes the catches to be inconveniently small. Even though these hauls were frequently too small to measure accurately, nevertheless, the upper limit of the richness of the population may be obtained from them. The abundance of the plankton as measured by the plankton sampler is summarized below:

	Coastal Area (Stations 1-4)	Off-shore Areas (Stations 5-9)
Total number of hauls	67	71
Number < 0.1 cc./m. <sup>3</sup>	15	51
Number > 1.0 cc./m. <sup>3</sup>	15	5
Average of cases 1.0-0.1 cc./m. <sup>3</sup>	0.54 cc./m. <sup>3</sup> (37 cases)	0.40 cc./m. <sup>3</sup> (15 cases)
Maximum abundance	15.5 cc./m. <sup>3</sup>	3.5 cc./m. <sup>3</sup>

The foregoing data point once again to the characteristically greater richness of the coastal area as compared with the offshore areas. Beyond the edge of the continental shelf the concentration of plankton was less than 0.1 cc./m.<sup>3</sup> in about 75 per cent of the cases whereas in the coastal area more than 75 per cent of the hauls indicated an abundance greater than 0.1 cc./m.<sup>3</sup>. All the catches greater than 2.0 cc./m.<sup>3</sup> in the coastal area and greater than 1.0 cc./m.<sup>3</sup> in the offshore areas were dominated by salpae. Since in the coastal area an equal number of very large and very small hauls were taken, we may regard the majority of catches of intermediate size (1.0-0.1 cc./m.<sup>3</sup>) as typical of this region. The average of the cases which fell in this category (almost all of which occurred in the warmer half of the year) is 0.54 cc./m.<sup>3</sup> and may be compared with the estimate of the absolute abundance of the plankton in this area made by Bigelow and Sears and based on hauls with 1-meter

nets. These investigators reported averages of "about 0.5–0.8 cc. per cubic meter at the season of maximum production." These two estimates, reached by very different methods, agree so closely that we are led to place considerable reliance on the order of magnitude of the values obtained as an index of the actual richness of plankton in this coastal region (cf. Clarke, 1939*b*).<sup>6</sup> The fact that our average value is found to be at the lower limit of the range given by Bigelow and Sears adds support to the conclusion reached above that the period of the present investigation was one of relative plankton scarcity.

A further evidence that the plankton under consideration here differed significantly from that present during the period of the earlier investigation is furnished by the unusual abundance of salpae which we encountered. Bigelow and Sears reported that salpae, medusae and ctenophores ordinarily accounted for only a small percentage of the entire catch but that a maximum value of 22 per cent for the area as a whole was found in June, 1932. In our hauls, however, the total plankton for the four coastal stations combined amounted to more than twice the volume of the crustacean plankton on 6 out of the 10 cruises and on certain occasions it was several times more abundant. The inference is that during the period from October, 1937 to June, 1939 in our coastal area the plankton as a whole was relatively scarce and that the crustacea were particularly depleted, while the other elements—especially the salpae—were unusually abundant. The recurrence of such important differences in both the quantity and the complexion of the plankton in the waters over the continental shelf and their undoubted significance in the ecology of the region is further elaborated elsewhere (Sears and Clarke, 1940).

As yet we have no adequate information on the possible occurrence of annual variations in the plankton in the slope water area or in the regions farther offshore. Further quantitative investigation is demanded. Nevertheless, it is doubtful whether the plankton beyond the edge of the continental shelf ever reaches the proportions of that within the coastal area. What factor essentially underlies the differences in the richness of the standing crop in the three areas remains to be worked out. The characteristic differences in depth and the seasonal changes in temperature, which have been described above, determine what portion of the whole water column can be effectively stirred and thus bring about a regeneration of nutrients and a renewed impetus to biological production. But the details of these events are not yet adequately

<sup>6</sup> The agreement also adds support to the conclusion of Clarke and Bumpus (1939) and of Winsor and Clarke (1940) that a plankton net only 5 inches in diameter is as reliable as a meter net for a quantitative measure of the plankton.



known and much remains to be learned of the rates of reproduction and growth of the dominant organisms in these areas before the characteristic annual productivity of each can be ascertained. Nevertheless, the present observations make it clear that a distinct difference in the richness of the plankton of the three areas existed during the period of this investigation and since the indications are that this period was one of relative scarcity for the coastal area, we may suspect that the ratio of plankton abundance in waters over the continental shelf to that farther offshore is in general even greater than was found in the present case.

#### SUMMARY

1. The abundance of the zoöplankton in the coastal water, the slope water, and the Sargasso Sea at stations between Montauk Point, N. Y., and Bermuda was investigated over a period of a year and a half by means of shallow and deep hauls made chiefly with 75 cm. scrim nets. Analysis of the plankton by volume measurement and by enumeration revealed that wide variations both in the quantity and in the composition of the hauls occurred within short periods of time and within relatively short distances.

2. A noticeable diurnal migration of the crustacean plankton was detected in the coastal water and particularly in the slope water, although the vertical distribution of the plankton as a whole was not significantly affected by diurnal movement. When all observations are combined, the surface layers do not appear to have been generally richer than the deeper strata except in the case of the Sargasso Sea station.

3. An unexpectedly great seasonal difference in the abundance of the plankton was revealed, the volume of the catches in the warm half of the year being as much as 20 times or 40 times greater than in the winter in the coastal area and as much as 10 times greater in the slope water area, but no significant seasonal change was indicated in the Sargasso region.

4. When the shallow and deep hauls throughout the year are combined, the investigation as a whole shows that the average volume of the plankton was about 4 times greater in the coastal area than in the slope water area and that the latter was about 4 times greater than at the Sargasso Sea station. Differences in the same direction but of smaller magnitude were found for the crustacean plankton.

5. Individual study of *Calanus finmarchicus* and of *Centropages typicus* showed that the abundance of these copepods, which were confined to the coastal area, fluctuated widely, the former being most numerous in spring and early summer and the latter in late summer and autumn.

6. The actual richness of the plankton in the coastal area as measured by the plankton sampler fell within the approximate range observed by earlier investigators, but all indications point to the period of the present study as one of relative scarcity. In addition, the proportion of the crustacea in the hauls was unusually low (less than half the total plankton in 6 out of 10 cruises) and the number of salpae was unusually high. The superiority in richness of the coastal area over the offshore areas probably is generally even greater than that found in the present case.

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